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CHAPTER 29

BIOLOGICAL PROCESSES AFFECTING THE DISTRIBUTION OF POLLUTANTS IN MARINE SEDIMENTS, PART II. BIODEPOSITION AND BIOTURBATION

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INTRODUCTION

Activities of benthic organisms modify the physical and chemical nature of marine sediments. This chapter examines the rates and mechanisms of biodeposition and bioturbation in relation to the fate and transfer of pollutants. It constitutes the second part of a review on biological processes affecting the distribution of pollutants. Part I covered bioaccumulation, trophic transfer, migration and biodegradation (see Chapter 28, this volume). The major emphasis in this review is on biological alterations of sediments and their chemistry rather than sediment effects on the biota. The latter topic, as well as other aspects of organism-sediment interactions, is covered in other reviews [1-9].

In this chapter we will summarize the fundamental literature on organism-sediment interactions and compile rates of various processes, emphasizing differences in the rates and mechanisms of sediment modification among groups of functionally similar species (i.e., guilds). We believe such a review can promote a better understanding of the fate and transport of pollutants in several ways. In areas where the dominant sediment reworkers are known, the information may be sufficient to allow qualitative or semiquantitative predictions concerning the distribution of pollutants. A mechanistic approach also allows limited qualitative

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predictions about habitat, biogeographical and seasonal differences in the relative importance of various processes. Finally, the functional differences among guilds may serve as a rationale for choosing species for detailed field or laboratory study.

FEEDING-MOBILITY CLASSIFICATION

The effect of a benthic organism on sediment structure and chemistry depends on its mode of feeding, locomotion and relation to the substrate. In this section we propose a classification of benthic invertebrates in relation to bioturbation processes. Organisms are grouped according to three dichotomies: epifaunal/infaunal, mobile/stationary and deposit/suspension feeding. We thus recognize 12 guilds of organisms based on these criteria (Table I). For several of these guilds, tubicolous and nontubicolous subgroups could be recognized, but are not included to minimize the number of groups. Carnivores and rare feeding types are not included because their low densities generally preclude major effects on sediment structure. We recognize the inherent limitations in this kind of classification due to the plasticity of feeding behavior of many invertebrates.

Epifauna include species that feed on the surface but occasionally burrow into the sediment, e.g., gastropods. In our classification, mobile fauna are those that move through the sediment on a regular basis, thereby disrupting sediment structure. Species that move in frequent episodic events followed by a relatively stationary period, e.g., some tubicolous nereids, are considered mobile. Jumars and Fauchald [10] classified such species as "discretely mobile." Fauna that move only during times of stress or reproduction are not considered mobile. Mobile fauna are separated into "vagile" species and "excavators." Vagile fauna burrow through the sediment by displacement of particles, which may create temporary gaps or burrows. Common vagile taxa include mobile bivalves and many errant polychaetes. Excavators move through the sediment by digging semipermanent or permanent burrows. Decapod crustaceans, such as *Uca*, *Callianassa* and *Nephrops*, are common excavators. Certain errant polychaetes combine vagile and excavator modes by making semipermanent and temporary burrows, e.g., *Scoloplos* [11] and *Glycera* [12]. As more sediment is displaced by the temporary burrows, such species are considered vagile.

Tubes are domiciles that differ from temporary or permanent burrows in several respects. Most permanent tubes are either secreted or constructed from sediment selected at the sediment surface [13-16]. Burrows represent a modification of surrounding sediment. Tube structure by any species is relatively fixed compared to the considerable conspecific variation found in burrows. Finally, total volume and free volume (space not utilized by the occupant) tend to be larger in burrows than in tubes.

The first dichotomy in feeding type is between suspension-feeders, which ingest particles located in the water column, and deposit-feeders, which ingest

Table I. Feeding-Mobility Classification and Sediment Modifying Processes for Each Guild

Classification (Guilds)	Guild Abbreviation	Representative Taxa	Feeding Zone	Particle Reworking From:			Biodeposition	Pelletization	Tubes	Fluid Transport
				Feeding	Burrowing	Excavation				
I. Suspension-feeders										
IA. Filter-feeders	FF									
Mobile infaunal	MIFF	*Mya, Mercenaria*	Bottom few cm of water column	0[a]	+[b]	0	+	+	0	++[c]
Stationary infaunal	SIFF	sabellids, phoronids	Bottom few cm of water column	0	0	0	+	+	+	+
Stationary epifaunal	SEFF	*Crassostrea, Mytilus*	Bottom to several meters into water column	0	0	0	++	++	0	0
IB. Raptorial feeders	RF	cerianthids, corals	Bottom to several meters into water column	0	0	0	+	0	0 (+)[d]	0 (+)
II. Deposit-feeders										
IIA. Surface deposit-feeder	SDF									
Mobile infaunal SDF-vagile	MISDF-V	*Tellina, Macoma*, cirratulids, nereids	0–1 cm of sediment	+	+	0	0(+)	+	0 (+)	+
Mobile infaunal SDF-excavator	MISDF-E	*Uca*	0–1 cm of sediment	++ ?	0	++	0	++ ?	0	++
Stationary infaunal SDF	SISDF	spionids, onuphids	0–1 cm of sediment	+	0	0	0(+)	+	+	+
Mobile epifaunal SDF	MESDF	*Amphitrite, Hydrobia*, holothurians	0–3? cm of sediment	+ (++)	+	0	0	++	0	0
IIB. Subsurface Deposit-feeder	SSDF									
Mobile infaunal SSDF-vagile	MISSDF-V	*Yoldia, Nucula, Scoloplos, Nephtys*	0–>20 cm of sediment	+	++	0	0	++	0	++
Mobile infaunal SSDF-excavator	MISSDF-E	*Callianesa, Upogebia*	0–>1 m of sediment	++	0	++	0 (+)	+ (++)	0	++
Funnel-feeders	FUN	*Leptosynapta, Arenicola Balanoglossus*	Predominantly upper 0–1 cm, down >10 cm	++	+	0	0	0	0	++
Conveyor-belt species (= stationary SSDF)	CB	*Pectinaria, Clymenella Molpadia*	Deeper sediment 3–30 cm	+ (++)	0	0	0	+?	+	+ (++)

[a] 0 = process absent or normally of minor importance in modifying sediment.
[b] + = process present in at least some species and moderately to highly significant in modifying sediment.
[c] ++ = process present in at least some species and of major significance in modifying sediment.
[d] ( ) = indicates occasional importance or importance for subset of species within guild.

organic and inorganic particles on or in the bottom. Most suspension-feeders are filter-feeders, that is, they capture suspended particles by filtering water through gills or other types of sieving structures [17]. Raptorial suspension-feeders capture prey by means other than filtering, e.g., nematocysts in anthozoans.

Deposit-feeders are divided into species feeding at the sediment-water interface (surface deposit-feeders) and those feeding below the sediment surface (subsurface deposit-feeders). Surface deposit-feeders collect surficial sediments with tentacles, palps, siphons, mouth parts and chelae, although several surface deposit-feeding polychaetes and bivalves also filter-feed to some extent [18,19]. Subsurface deposit-feeders utilize a wide variety of feeding mechanisms, ingest sediment from <1 cm below the surface to depths >20 cm, and include most mobility and tube types. Previous classifications have often labeled surface deposit-feeders as "selective deposit-feeders" and subsurface deposit-feeders as "nonselective deposit-feeders." The present classification system makes no *a priori* assumptions about the degree of particle selectivity.

Two methods of subsurface deposit-feeding require special attention. Funnel-feeders, a mobile group, ingest sediment at one end of an L- or U-shaped burrow and defecate at the other end, either at the surface or in old burrows [20]. A funnel-shaped depression forms at the anterior end as a result of slumping of surface sediment. The funnel is a mechanism to exploit the organically rich surface layers [20]. Conveyor-belt species are vertically oriented in the sediment with head end down and the posterior located at or near the surface [5]. These species ingest deeper sediments and deposit them as feces at the surface, resulting in the exposure of deep sediment and the burial of the surficial layer. Except for *Pectinaria*, conveyor-belt species appear to be stationary and are classified in Table I as stationary subsurface deposit-feeders.

BIODEPOSITION

As a sedimentary process, feces production by deposit-feeders is qualitatively different from that of filter-feeders. Fecal pellet production by deposit-feeders changes sediment characteristics and microbial activity but does not add new material to the sediment. By contrast, feces from pelagic and benthic filter-feeders are a source of new sedimentary material. The term "biodeposition" is thus restricted to the deposition of feces and pseudofeces by filter-feeders [21]. Pseudofeces are particles ejected before reaching the gut. Both filter- and deposit-feeders may produce pseudofeces. Many filter-feeders remove particles as fine as 1–5 μ [17,22]. Particles <4 μ composed 82-93% of the feces of oysters and mussels [23]. Haven and Morales-Alamo [23] calculated that 2- to 3-μ particles settle at a rate of 6.4×10^{-5} cm/sec whereas fecal pellets settle at 0.4–1.7 cm/sec. Although this comparison does not account for flocculation, the four orders of magnitude difference in settling rates indicates the potential importance of

biodeposition as a sedimentary process. Because of the faster settling rates of larger particles, biodeposition has the greatest impact on particles 1-50 μ in diameter. Removal of fine particles is especially important because they often have the greatest concentration of pollutants. Biodeposition by benthic organisms increases the rate of input of particulate or sorbed pollutants into the bottom, reduces their dispersal through currents, and concentrates fine particles in areas of higher wave or current energy. A similar role has been suggested for pelagic filter-feeders [24-27].

Few quantitative rates of biodeposition by benthic suspension-feeders are available; those in Table II are for bivalves. It appears that epifaunal filter-feeders, such as oysters, generally have greater biodeposition rates than infaunal species. This reflects both the larger size of epifaunal bivalves and a higher biodeposition rate per gram of body weight in epifaunal than infaunal bivalves [23,29]. We suspect that the rate of biodeposition is related to body weight in a logarithmic manner, as found for filtration rates [34,35] and egestion rates of deposit-feeders [36].

In the field, biodeposition varies as a function of several environmental factors. As expected, biodeposition rates decrease at low temperatures on the basis of temperature effects on invertebrate metabolism. Biodeposition by *Crassostrea virginica* at 6.7°C was only 15% of the summer rate and essentially stopped at <2.8°C [21]. Filtration and biodeposition rates are a function of seston levels [29,33,37]. At very high seston levels, certain species (*Mytilus edulis*) increase the rate of pseudofeces production, whereas other species (*Cerastoderma edule* and *Venerupis pullastra*) drastically reduce filtration rates [37].

Deposition by benthic filter-feeder populations can be a significant source of particulates, nutrients and pollutants (Table II). It has been suggested [21] that *Cardium* and *Mytilus* populations annually deposit 100,000 and 25,000-75,000 metric tons, respectively, in the Wadden Sea. At the other extreme, Myers [11] found that biodeposition was negligible in a sand community. Because feces often contain more organic matter than surface sediments [21,38] they may represent an important energy input [32] and may absorb metals or pollutants [39,40]. Annual input per square meter from the feces of *Geukensia* (=*Modiolus* or *Arcatula*) *demissus* in a Georgia marsh was 1.9 g K, 1.6 g N, 1.0 g Mg, 0.7 g P, 0.07 g Mn, 0.02 g Zn, 0.004 g Mo and 0.002 g Cu [30]. However, much of the filtered material may be resuspended particles, and biodeposition rates may overestimate net inputs.

The relative importance of biodeposition by infaunal, epibenthic and pelagic filter-feeders changes in different habitats (Table III). Biodeposition by benthic organisms should be higher in sandy than in muddy substrates because of the relatively low density of filter-feeders in most muds [4,5]. Exceptions to this generalization are oyster reefs and mussel banks, which can develop in soft

Table II. Biodeposition Rates

Species	Guild	Individual Rate (mg/ind./day)	Total Rate ($g/m^2/yr$)	Comments	Reference
Cardium edule	MIFF	648	-	Feces, wet weight	21
Cardium edule	MIFF	420	-		28
Crassostrea virginica	SEFF	$\bar{x}$ = 231 MAX = 560	2.8 kg 2.8 g P	Feces and pseudofeces, April-October	21
Crassostrea virginica	SEFF	4.7	-	Ash-free weight, feces and pseudofeces?, 0.586 g-dry wt oyster	29
Geukensia (=Modiolus) demissus	SEFF	126	-	Feces	21
Geukensia (=Modiolus) demissus	SEFF	235	549	Feces and pseudofeces, recalculated	30
Geukensia (=Modiolus) demissus	SEFF	-	1.9 g P	P content of feces and pseudofeces	31
Mercenaria mercenaria	MIFF	-	759 kcal	Energy content of feces and pseudofeces	32
Mercenaria mercenaria	MIFF	4.3	-	Ash-free weight, feces and pseudofeces?, 0.850 g-dry wt clam	29
Mya arenaria	MIFF	25	-	Feces	21
Mytilus edulis	SEFF	240-5400	-	Pseudofeces, 7 cm mussel, seston range 12-280 mg/l	33
Mytilus edulis	SEFF	4.3	-	Ash-free weight, feces and pseudofeces?, 0.475 g-dry wt mussel	29
Polymesoda caroliniana	MIFF	30	1.1	Feces and pseudofeces, recalculated	30

Table III. Habitat Differences in Sources of Fecal Pellets and Potential for Pelletization

Habitat/ Feeding Mode	Infaunal Filter-feeders	Epifaunal Filter-feeders	Pelagic Filter-feeders	Deposit-feeders	Pellet Breakdown Rate	Potential for Pelletization
Sand - Muddy Sand	0[a] to ++[b]	0 (+)[c,d]	Variable	+	Moderate to rapid	0 (+)
Muds	0[d]	0	Variable	++	Slow	+ (++)
Marshes	0	++	0	+	Slow	+
Deep Sea	0	0	+	+	Slow	?

[a] 0 = minor source of fecal pellets or potential for pelletization, low.
[b] ++ = major source of fecal pellets or potential for pelletization, very high.
[c] + = significant source of fecal pellets or potential for pelletization, moderate to high.
[d] ( ) = indicates an occasional rate or process.

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sediments. Because of the abundance of epifaunal filter-feeders in marshes, biodeposition is "rivaled in importance only by the formation of organo-clays" [41]. Density of zooplankton is not closely coupled with substrate type, so we expect that biodeposition by pelagic filter-feeders constitutes a relatively greater percentage of the input in muddy than in sandy habitats. Abundance of benthic filter-feeders is low in the deep sea [42], so biodeposition by zooplankton is much greater than by the benthos.

BIOTURBATION

Vertical Sediment Stratification

The sediment system can be divided into three layers: (1) the surface oxidized layer; (2) a deeper reduced layer; and (3) a transition layer. The surface layer contains free O_2, CO_2, $SO_4^=$, NO_3^- and ferric oxides, which impart a yellowish-brown color to the sediment. Free sulfides (H_2S, HS^-) are rapidly oxidized in this zone, except in certain microhabitats [43]. Redox potential (Eh) is positive and ranges from about +400–+100 mV. Deeper sediments constitute an anaerobic environment termed the sulfide system [44]. Anaerobic heterotrophs produce a variety of reduced end products of which hydrogen sulfide is the most important, but which also include NH_3, CH_4 and simple organic compounds [44]. Iron sulfides give the sediment its characteristic grey or black color. Redox potential ranges from about -100–-250 mV. The interface between the oxidized and reduced habitats is the redox potential discontinuity (RPD) layer [44]. This boundary layer is characterized by a rapid decrease in Eh with depth. Both O_2 and H_2S are present in the RPD, and Eh values are typically +100–-100 mV.

Bioturbation can modify patterns of horizontal stratification and affect the transport of particles and pollutants between sediment layers. In turn, the stratification characteristics influence the kinds of organisms and biological activities that can occur in the sediment.

Particle Transport

Various biogenic activities transport particles, their sorbed ions and entrapped pore water in both horizontal and vertical directions. The most important activities resulting in the transport or reworking of particles are feeding, burrowing, excavation and tube construction. Each of these activities has a different effect on the rate and direction of particle transport. In this section we review the rate and depth of particle transport and differences in transport processes among guilds (Table I).

The rate of particle reworking has been measured as the volume or weight of sediment transported per unit time, e.g., mg/day; thickness of the sediment

layer reworked per unit time, e.g., cm/day; time per year to turn over a sediment layer; or as an eddy diffusion coefficient, cm^2/sec. To facilitate comparisons between studies, we recommend that bulk density of the sediment and depth of the reworked layer be reported to allow conversion between units. Rate of reworking, in mg/ind./day, depth of the reworked layer and total reworking rate for the population in g/m^2/yr, are presented in Table IV. Values in Table IV were taken or converted from the original references or taken from compilations in Hargrave [36] or Powell [20]. A bulk density of 1.65 g/cc is used in all calculations where density is not specified. These sources do not always agree because different conversion factors were used. In some cases, the rates are for the total amount of sediment transported; in others, they represent only a specific activity, e.g., egestion. Since reworking rates are strongly temperature dependent [11,20,36,53,58], yearly rates that do not account for seasonal changes in reworking are most likely overestimates. Even with these limitations, the values in Table IV indicate the relative effect of different species and are sufficiently accurate for a first-order approximation of the amount of biogenic transport at sites with similar species.

Deposit-Feeding

Epifaunal surface deposit feeders include gastropods, echinoids, asteroids and holothurians. Epifaunal holothurians have some of the highest reworking rates for any guild, although feeding appears limited to the upper few centimeters, causing little vertical transport. Feces are deposited on the surface in elongated fecal ropes. Soft-bottom epifaunal holothurians are rare in the temperate zone but are abundant locally in the tropics [70] and deep sea [71]. Individual reworking rates of surface-feeding gastropods are very low, although they can be extremely abundant in intertidal and shallow water areas [59]. Feeding depth of gastropods is limited to the surficial layer; *Hydrobia* utilizes the upper 2 mm [59].

Vagile surface deposit-feeders include several common bivalves (*Macoma, Tellina, Scrobicularia*), which have moderate-to-high rates of reworking, and other taxa (cirratulid polychaetes, amphiurid ophiuroids), which appear to have relatively low feeding rates. Levinton [72] estimated the feeding depth of *Tellina agilis* and *Macoma tenta* as 0–5 mm. In many of these surface deposit-feeding bivalves much of the processed sediment is ejected as pseudofeces [56,73]. *Scrobicularia plana* egests up to 300 times as much pseudofeces as feces [73]. The only egestion rates for excavating surface deposit-feeders are for *Uca*, which are relatively low. Fiddler crabs and other surface deposit-feeding crabs are sufficiently dense in marshes to constitute a significant source of sediment reworking [30]. Many sedentary surface deposit-feeding taxa are small, e.g.,

Table IV. Individual Particle Reworking Rates, Annual Reworking Rates and Depth of Reworking

Species	Guild	Individual Reworking Rate (mg/ind/day)	Total Reworking Rate ($g/m^2/yr$)	Depth of Reworking	Comments	Source	Reference
Annelids							
Abarenicola claparedi	FUN	3,600	–	–	Average high and low tide, 1–3.5 g/ind.	O[a]	45
Abarenicola pacifica	FUN	10,900	–	–	Average high and low tide, 1–3.5 g/ind.	O	45
Abarenicola pacifica	FUN	0–4,500	–	–	0.7 g/ind., 9°C	O	46
		0–15,000	–	–	2 g/ind., 9°C	O	
		–	309 kg	≤15 cm	Site 3, mean 3 samplings	C[b]	
Amphitrite ornata	SISDF	5,100	–	Surface	≈17°C	O	16, 47
Amphitrite ornata	SISDF	2,600-5,200	–	Surface	22°C	O	16
Arenicola marina	FUN	4,700	–	–	Average of field measurements	O	48
Clymenella torquata	CB	900	54,282	20 cm	11°C	O	47
Clymenella torquata	CB	1,650	73,062	20 cm	Beaufort, North Carolina, annual rate adjusted for T°	C	49
Euzonus (=Thoracophelia) mucronata	MISSDF-V	230	–	–		O	50
Melinna palmata	SISDF	288	–	Surface	Cephalic plate width 2-8 mm, all sediment	P[c]	51
Pectinaria californiensis	CB	0.5–328	8,600	5 cm	Cephalic plate width 2-8 mm, all sediment	O	52
Pectinaria gouldii	CB	6,000	6,000	6 cm	All sediment, annual rate adjusted for T°	O	53
Pectinaria gouldii	CB	2,000	–		Just feces	O	53
Polycirrus eximius	SISDF	7	0–173	Surface	Just feces, April-October	C	11
Tharyx acutus	MISDF-V	7	0-1,316	Surface	Just feces, April-October	C	11
Scoloplos robustus	MISSDF-V	99	1,212-10,742	2–13 cm	Ingestion, April-October	C	11
		512	6,237-56,133		Burrowing, April-October		
Freshwater oligochaetes, 3 species	CB,MISSDF-V	1-250	18–230 kg	4–6 cm	Just feces, annual rate adjusted for T°	O	54
Bivalves							
Macoma balthica	MISDF-V	1.7	415	Surface	Just feces, 10°C, annual rate not adjusted for T°	O	55
		370	90,500		feces and pseudofeces, 10°C	O	
Macoma balthica	MISDF-V	520	–	Surface	feces and pseudofeces, 15°C	O	55
Macoma nasuta	MISDF-V	15–552	–	1 mm	Just feces, 10–50 mm/ind.	O	56
		7,272			feces and pseudofeces, 48 mm/ind.		
Scrobicularia plana	MISDF-V	14,400	–	Surface	feces and pseudofeces	P	57

Bivalves (continued)							
Scrobicularia plana	MISDF-V	3.9–90	–	Surface	Just feces	H[d]	57
Yoldia limatula	MISSDF-V	282	2,262	2 cm	Feces and pseudofeces	O	47, 58
Gastropods							
Hydrobia minuta	MESDF	1	26–8871	2 mm	Annual rate not adjusted for T°	O	59
Hydrobia ventrosa	MESDF	1	0–12,317	2 mm	Annual rate not adjusted for T°	O	59
Littorina irrorata	MESDF	0.4	107	Surface	Just feces, recalculated from data	C	30
Crustaceans							
Callianassa californiensis	MISSDF-E	33,000–82,500	–	<76 cm	Amount deposited per entrance, excavation and feeding?	C	60
Callianassa major	MISSDF-E	3,472	12.6–633 kg	–	Amount deposited per entrance, just feces	O	28
Callianassa sp.	MISSDF-E	–	5,577 kg	–	30 *Callianassa* burrows/m^2, Jamaica	C	61
Haustorid amphipods, 6 species	MIFF	277–9,900	–	<2.5 cm to <10 cm	Burrowing	C	62
Paraphoxus spinosus	MISDF-V	8,910	54.4–2,159 kg	0–1 cm	Burrowing	C	11
Uca pugillator	MISDF-E	96	231	–	Just feces, recalculated from data	C	30
Uca pugnax	MISDF-E	75	821	–	Just feces, recalculated from data	C	30
Echinoderms							
Caudina chilenses	CB	157,700	–	–		P	63
Echinocardium cordatum	MSSDF-V	2,959	–	–		P	64
Holothuria spp. 7 species	MESDF	24,657–224,657	–	–		P	65, 66
Leptosynapta tenuis	FUN	10,400–18,430	–	0.5–10 cm	Feces and below surface reworking	O	20
Leptosynapta tenuis	FUN	33,825	585–2,924 kg	1.15 cm	Feces and below surface reworking	C	11
Scotoplanes sp.	MESDF	100,000	–	1 mm	Feces	O	67
Stichopus moebii	MESDF	37,534	–	–		P	68
Stichopus variegatus	MESDF	49,315	–	–		P	63
Enteropneust							
Balanoglossus gigas	FUN	200,000–250,000	–	–		P	69

[a]O = original data [b]C = calculated from data. [c]P = calculated by Powell [20]. [d]H = calculated by Hargrave [36].

spionids, and appear to have low-to moderate reworking rates. An exception is *Amphitrite ornata*, a large terebellid polychaete [16,47].

Two major groups of the vagile subsurface deposit-feeders are protobranch bivalves (*Yoldia, Nucula*) and polychaetes, e.g., orbiniids, nephtyids, some nereids, opheliids and some capitellids. Protobranchs are dominant reworkers in several subtidal muddy habitats [5]. *Yoldia limatula* moves through the upper 4 cm of sediment, drawing in particles with its palps and egesting sediment at the surface [74,75]. As a result of feeding, surface sediment is subducted, while deeper sediment (2-4 cm) is transported to the surface or resuspended. *Nucula* feeds in a similar fashion but less deeply. Levinton [72] measured the feeding depth of *Yoldia limatula* as 23.7 mm and that of *Nucula proxima* as 7.9 mm. Production of fecal pellets by protobranchs can have a pronounced effect on sediment structure, as discussed later. The relatively low feeding rates for active (*Euzonus mucronata*) and large (*Scoloplos robustus*) polychaetes suggests that ingestion by polychaetes is lower than by protobranch bivalves. However, deeper sediments may be transported by polychaetes than protobranchs because several species feed, or at least burrow, at depths of >15 cm [76-78].

The most prominent taxon among the excavating subsurface deposit-feeders are the thalassinid crustaceans, e.g., *Callianassa, Upogebia*. Several studies have demonstrated that thalassinids are primarily deposit-feeders, rather than filter-feeders [60,79-81]. *Callianassa major* produces 3472 mg/day of feces per burrow entrance [28], which is relatively high compared to other subsurface deposit-feeders. However, this rate is much less than the total reworking rate of *Callianassa californiensis* (52,000-132,000 mg/day sediment per burrow entrance [60]), suggesting that excavation is the dominant transport mechanism. *Callianassa* and *Upogebia* are abundant in Georgia, Florida and the Gulf of Mexico in habitats ranging from lagoons to the continental shelf [28,82], as well as on the Pacific coast [60,83] and in the Caribbean [61,84]. Where abundant, thalassinids are the dominant sediment reworker.

Powell [20] computed a sediment budget for *Leptosynapta tenuis*, a burrowing holothurian, which may apply to other funnel-feeders. *Leptosynapta* ingests surface sediments, which slide down the feeding funnel; 51% of the ingested sediment was from the 0- to 0.5-cm layer and 75% from 0-3 cm. Approximately 45% of the ingested sediment was deposited in a fecal mound and thereby subject to erosion. Funnel-feeders differ from other deposit-feeders by transporting sediment downward as well as upward during feeding. Of the total sediment budget for *Leptosynapta*, 23% was transported downward, resulting in a yearly transport of 453–863 g from the top 0.5 cm to deeper layers. The feeding mechanisms of lugworms (*Arenicola* and *Abarenicola*) [45,46,48] and *Balanoglossus gigas* [69] appear similar to that of *Leptosynapta*, except that these taxa are often 20–40 cm below the surface. Both *Leptosynapta* [11] and

the lugworms [46,85] can be very abundant in sandy intertidal areas and are the dominant sediment reworkers in such areas.

Conveyor-belt species transport deeper sediments to the sediment–water interface and, over time, subduct the previous surface layer to their feeding depth. Reworking rates of *Pectinaria* and *Clymenella* are great enough to result in moderately rapid sediment turnover [47,53]. Feeding depths range from 1 cm for juvenile *Pectinaria gouldii* [86] to ⩾20 cm in *Molpadia oolitica* [87].

Aller and Dodge [61] illustrated the redistribution of a pulsed input, e.g., particulate pollutant, by vertically oriented deposit-feeders. Deposition of feces and excavated sediment at the surface covers the polluted layer and protects it from erosion [88]. The polluted surface layer sinks at the combined rate of biogenic deposition and abiogenic sedimentation, although the latter is often insignificant. Once the previous surface layer reaches the feeding depth, it is ingested and returned to the surface. Over several cycles the pollutant is homogenized within the reworked layer. However, if all or a portion of the particles are of an unsuitable size for ingestion, they are concentrated at the feeding depth as a lag deposit. Such biogenic graded bedding appears to be a common occurrence where conveyor-belt species or funnel-feeders are abundant [47,85, 87,89]. Many conveyor-belt species or funnel-feeders "avoid" particles >1 mm [11,46,47,85], leaving the very coarse sand fraction and larger particles concentrated in layers. *Leptosynapta tenuis* [20] and *Pectinaria gouldii* [86] "avoid" very fine particles, which can have the effect of retaining fines in areas of large mean grain size.

Tube Construction and Excavation

During construction and maintenance of arenaceous or muddy tubes, the occupant selects suitable particles from the sediment surface, resulting in a downward transport of surficial particles [13-16]. In a sand community with a high density of tubicolous taxa, tube building accounted for 6.8–17.5% of the total sediment reworking and 10.8–23.4% of the reworking in the top 1 cm [11]. Much of the surface sediment may be bound in tubes [90]. Since many tubicolous species are limited to the upper 1–5 cm, only shallow vertical transport occurs. Species that make deep (⩾20 cm), muddy tubes, e.g., *Amphitrite ornata* [16] and certain other ampharetid and terebellid polychaetes, are exceptions. Particle selection also can result in localized concentrations of specific mineral types or size fractions [13,90].

By contrast to tube construction, excavation of semipermanent burrows causes net upward transport of sediment. In this way, excavators, regardless of feeding type, resemble conveyor-belt species. However, excavators transport sediment from the total depth of the burrow, rather than just one depth, and probably demonstrate less particle selectivity. Excavation by decapods is the

deepest penetrating form of bioturbation. Several species of decapods common in Georgia salt marshes excavate burrows from <10 cm to >65 cm deep [91], whereas thalassinid burrows are from ≤100->300 cm deep [60,84,92]. Where abundant, excavators will set the lower depth of the bioturbated layer. As mentioned previously, rates of sediment working by *Callianassa* are extremely high [28,60,61]. Species of thalassinids that do not produce sediment mounds may have lower reworking rates than those that produce mounds. Where moderately abundant, thalassinids are the dominant sediment reworkers and homogenize the upper ≈20-100 cm. Although rates of burrow excavation apparently are unkown, salt marshes and mangrove forests are riddled by decapod burrows. In Georgia, density of burrow apertures ranged from 250 m^{-2} to 1040 m^{-2} in different salt marsh zones [91]. Excavation by *Uca* and other marsh crabs probably is not as great as by the thalassinids, but still plays a significant role in transporting deeper sediment to the surface. For example, sediment-bound oil was brought to the surface by excavation of burrows by recolonizing fiddler crabs, *Uca pugnax* [92].

When abandoned burrows are filled in, localized concentrations and downward transport of surface sediments to depths of ≥1 meter can result. Filled burrows commonly occur in both shallow water [84,93] and the deep sea [94, 95]. In a polluted site, filled burrows of a thalassinid had "anomalous concentrations of lead, zinc, copper, and iron" [93].

Burrowing

The influence of burrowing on sediment transport depends on the cross-sectional area of the burrower, distance burrowed and, perhaps, the velocity of burrowing. *Scoloplos robustus* and various amphipods displace a large amount of sediment during burrowing (Table IV), although it is likely that particles are moved only short distances either laterally or posteriorly. Hence, reworking rates calculated for vermiform taxa or small crustaceans may overestimate their influence on particle transport and sediment structure. The lack of any effect on sediment compaction by *Scoloplos robustus* [11] supports this suggestion and should caution researchers not to use sediment reworking rates as the sole method of predeicting a species' effect. Burrowing bivalves may have a greater impact on sediment structure because of their greater size and, in some cases, mobility, e.g., *Yoldia*. It appears that burrowing does not affect particle transport as much as feeding, excavation or perhaps tube construction. This may not be the case with fluid transport, as discussed later.

Epibenthos

Epibenthic invertebrates and demersal fishes disturb sediments by their locomotive, food-gathering and burrowing activities. The most impressive

examples of such disruption are the depressions excavated by sting rays, which can exceed 1 meter in diameter and 30 cm in depth [96,97]. Pockets of recent sediment may form in such depressions. Rhoads [47] found that the horseshoe crab (*Limulus polyphemus*) and moon snail (*Polinices duplicatus*) reworked the upper 3–10 cm in artifically laminated sediments. Other burrowing epibenthic taxa, e.g., *Callinectes*, shrimp, flatfish, are often quite abundant and play a significant, although largely unmeasured, role in mixing the upper 1–10 cm. Schafer [3] discussed the types of sediment disruptions caused by epibenthic species.

Biogenic Mixing Coefficients

Another approach to quantifying biogenic reworking is to treat it as an eddy diffusion process [7,9,98-100]. This approach assumes that the rate of mixing of particles (or fluids) does not vary either horizontally or vertically within the biologically active layer. These conditions are not met when transport is advective or occurs in episodic events. When applicable, an advantage of the diffusion analogue is that it can be calculated from relatively easily measured chemical or physical parameters. This is especially advantageous in the deep sea. Another advantage is that it allows comparison of the rate of particulate, fluid and molecular transport.

One method of estimating the biogenic mixing coefficient is "dimensional analysis" [98]:

$$D = Lv_c$$

where D = biogenic mixing coefficient, cm x $cm^3/cm^2/sec = cm^2/sec$,
L = depth of mixed layer, cm, and
v_c = volume of sediment reworked per unit area per unit time or the apparent sedimentation rate, $cm^3/cm^2/sec = cm/sec$.

Other methods of calculating biogenic mixing coefficients are based on depth profiles of conservative or radioactive tracers [98,100] or from modeling of pore water profiles of dissolved ions [101,102].

Modeling of pore water profiles generates biogenic mixing coefficients for dissolved ions (an apparent, stochastic or effective diffusion coefficient) [101]. All these methods are based on certain largely untested assumptions, and it is not apparent how robust they are to violations.

Table V lists biogenic mixing coefficients for individual species and for the total community at various sites, as well as molecular diffusion coefficients for selected ions. Three conclusions are apparent from these data. First, the rate of particulate biogenic reworking is very low in the deep sea, on the order of 3.16×10^{-11}–3.16×10^{-8} cm^2/sec [98,100,104]. On average, deep sea

Table V. Biogenic Mixing Coefficients

Location	Species	L[a](cm)	D[b](cm²/sec)	Method	Reference
Deep Sea, various sites	?	10–48	3.16×10^{-11}–3.16×10^{-8}	Dimensional analysis	98
Mid-Atlantic Ridge	?	8	6×10^{-9}	^{210}Pb pattern	100
Long Island Sound	*Yoldia,Nucula*	4	1.2–3.5×10^{-6}	^{234}Th pattern	75
Chesapeake Bay	?	10–15	1×10^{-6}	Dimensional analysis?	103
New York Bight	?	?	5×10^{-7}	^{234}Th pattern	104
Rhode Island	*Leptosynapta, Scoloplos*				
0–1 cm		1	2.9×10^{-6}–1.6×10^{-5}	Dimensional analysis[c]	11
2–10 cm		8	8.3×10^{-7}–4.3×10^{-6}	Dimensional analysis[c]	11
La Jolla, California	*Euzonus* (=*Thoracophelia*) *mucronata*	30	1.5×10^{-5}	Dimensional analysis[d]	50
Barnstable Harbor, Massachusetts	*Pectinaria gouldii*	6	7.6×10^{-8}	Dimensional analysis[d]	53
Long Island Sound	*Yoldia limatula*	2	3.2×10^{-7}	Dimensional analysis[d]	58
Long Island Sound	*Yoldia limatula*	3	2×10^{-6}	Dimensional analysis[e]	58
Laboratory	*Yoldia limatula*	3	1×10^{-5}	Pore water profiles	101
Laboratory	*Clymenella torquata*	11	2–3×10^{-4}	Pore water profiles[f]	101
Laboratory	*Clymenella torquata*	11	4.5×10^{-5}	Pore water profiles[g]	101

Laboratory	*Molpadia oolitica*	7–9	$5.7–9.4 \times 10^{-5}$	Depth of oxidized layer[c]	87
Molecular Diffusion	NH_4^+	–	7×10^{-6}	–	101
Molecular Diffusion	Fe^{++}	–	2.4×10^{-6}	–	101
Molecular Diffusion	H_2S	–	1.4×10^{-5}	–	105
Molecular Diffusion	$SO_4^=$	–	1.0×10^{-5}	–	105
Molecular Diffusion	$SO_4^=$	–	$2.4–4.7 \times 10^{-6}$	–	102
Molecular Diffusion	^{106}Ru	–	$1 \times 10^{-11}–10^{-12}$	–	103

[a] L = depth of the reworked layer.
[b] D = biogenic mixing coefficient.
[c] Calculated from data.
[d] Calculated by Guinasso and Schink [98].
[e] Calculated by Aller [101].
[f] Vertical diffusion coefficient.
[g] Horizontal diffusion coefficient.

biogenic reworking rates are about two to three orders of magnitude lower than those in shallow water. This conclusion is consistent with the low density and metabolism of deep sea communities [67,106]. Deep sea rates are also several orders of magnitude less than rates of molecular diffusion, indicating that particulate biogenic reworking is insufficient to alter the pore water profiles or flux of most dissolved ions. Second, rates of molecular diffusion for NH_4^+, Fe^{++}, H_2S and $SO_4^=$ are as great as, or greater than, the particle reworking rates of several species or the total rate for most shallow water sites. Although the discrepancy is not as great as in the deep sea, this indicates that particle reworking per se normally has a minor influence on the distribution of these ions as suggested by Aller [9]. Certain molecules such as ^{106}Ru have much lower diffusion rates, and biogenic particulate transport controls the diffusion rates for such compounds [103]. As discussed later, biogenic fluid transport may have a greater impact on the pore water profiles of these ions. Finally, rates calculated for a sandy habitat in Rhode Island indicate a three- to fourfold difference in the particulate reworking between the surface layer (0–1 cm) and deeper layer (2–10 cm) [11]. Such vertical gradients in the rate of reworking probably occur in most communities not dominated by excavators or protobranchs.

Stabilizing Processes

A variety of biological processes stabilize sediment surfaces and increase sediment strength. These processes are the antithesis of most reworking activities because they decrease erosion and increase deposition of fines. The three most important stabilizing mechanisms are microbial binding, tubes and aquatic vegetation.

Microbial Binding

Microorganisms release a diversity of organic compounds as extracellular products and by autolysis. These organic compounds and, in particular, polysaccharides, bind terrestrial soils [107-109].

Recently, it has been suggested that polysaccharides are the principal binding agent in marine sediments [110,111]. Certain meiofaunal (e.g., nematodes [112]) and macrofaunal (e.g., nemerteans) groups also produce copious amounts of mucus, which may contribute to the binding of marine sediments.

Stability of a sediment appears related to its organic content and perhaps the nature of the organic compounds. Both Frankel and Mead [113] and Johnson [114] found that an organic matrix filled the interstices of marine muds and fine sands. This viscous gel bound the finer particles. Hulbert and Given [115] suggested that the "unexpected (shear) strength" in Gulf of Marine surface sediments was attributable to the presence of labile organics. In laboratory

studies, critical erosion velocity increased with carbon content of sediment [116] and shear strength increased with carbohydrate content [117]. Levels of carbohydrates in the latter study were high and may be atypical for marine sediments, which generally have lower concentrations of carbohydrates than terrestrial soils [118].

To date, only a few experimental studies have attempted to elucidate the role microbes have on the physical properties of sediments. In a set of flask experiments, mucilage-secreting benthic diatoms greatly reduced resuspension of silt-clays, as well as a mixture of 90% sand and 10% silt-clay [119]. However, none of the diatoms significantly reduced resuspension of fine sands without silt-clays. Nonmucilage-secreting diatoms had no significant effect on resuspension of any sediment. By removing and then incubating bacteria on sediment, Webb [120] demonstrated that the size, shape and adhesion of sand grains were modified by microbial films. Alteration of these properties in turn modified porosity and lattice structure of the particles. Growth of microbes on different sizes of glass beads reduced critical rolling velocity by 25-60% in a laboratory flume study [110]. Neither the absolute change nor the rate of change in the critical rolling velocity was obviously related to sediment size. Although the results of this experiment are provocative, it should be noted that replication with the same bead size gave substantially different values, and no control was conducted for compaction.

On the basis of these observations and experiments, we can tentatively conclude that microbial exudates are a significant, and perhaps major, source of sediment binding. Polysaccharides may be the major binding agent. Mucus production by meiofauna and macrofauna probably plays a secondary role in comparison to microbes. Exudates bind sediments by increasing adhesion at grain-to-grain contacts. Other mechanisms by which microbes and their by-products modify sediment properties are: (1) increased grain size, resulting in a new lattice structure; (2) filling of interstitial voids with a viscous fluid; (3) formation of a protective surface film; and (4) agglutinating fine particles into flocs.

The intensity of microbial binding varies both between habitats and seasonally. Microbial binding has its greatest impact on fine sands and silt-clays in lower energy environments. Holland et al.'s results [119] suggest that the presence of silt-clays is important in the binding process. Such an interaction could be the result of increased microbial densities due either to high surface area of silt-clays, or as a result of the silt-clay greatly increasing the number of grain-to-grain contacts. The low organic content and bacterial respiration in the deep sea suggest that microbial binding is low. Based on the seasonal fluctuations in benthic primary production [121] and microbial metabolism [122, 123], we expect that the rate of exudate production is highest in summer and lowest in winter. However, the net change in microbial binding represents

the balance between the rate of exudate production and the combined effects of destabilization by reworking and microbial decomposition of exudates [108]. As both stabilizing and destabilizing processes are temperature dependent, we do not expect to find a similar seasonal pattern in all communities. For example, surface microbial films occur in the summer in Long Island [124] and only during the winter in Rhode Island [11]. Organic binding of sediment also appears sensitive to pollution. Sanders [125] noted that sandy sediments become less stable after an oil spill "due to the breakdown and disappearance of animal secretions, tubes and benthic algae." Flume experiments similar to those conducted by Rhoads et al. [110], but with the addition of pollutants, could indicate the likely effects of waste disposal on sediment stability.

Tubes

Dense populations of tubicolous fauna can stabilize an otherwise mobile sediment, increase deposition of fines and alter the composition of the infaunal community. A dense settlement of the tubicolous polychaete *Owenia fusiformis* stabilized a shifting sand, which resulted in accretion of 5–10 cm of sediment [13]. Sediment erosion increased following destruction of the worm bed by sting rays. Dense settlement of the tubicolous amphipod *Corophium insidiosum* in a sandy habitat increased deposition of fine material, critical erosion velocity, and density and diversity of the other fauna [11]. In comparison to the relatively firm tubes of *Corophium*, the mucus tube-sheaths of *Prionospio heterobranchia* appeared to have little or no stabilizing effect [11]. Other cases of sediment stabilization and accretion due to settlement of tubicolous taxa have been reported for intertidal [90] and subtidal [110,126] habitats. In the only experimental study, introduction of *Heteromastus filiformis* into a laboratory flume increased critical rolling and suspension velocities [110], although there were no controls for time-related changes independent of tubes. This small capitellid polychaete makes a thin mucus-bound tube. Larger, less-abundant species may modify sediment characteristics around their tubes and increase sediment heterogeneity. Sediment shear strength was $\leq$1.9 times greater within a 20-cm radius of the tube of *Cerianthus* sp, a large burrowing sea anemone [67].

Mechanisms by which tubes modify sediment characteristics are poorly understood. Closely spaced tubes may increase shear strength by acting in a manner analagous to reinforcing rods. Large tubes, such as those made by *Cerianthus*, may modify surrounding sediment by decreasing water content and porosity. Rhoads et al. [110] proposed four mechanisms to explain the increase in critical erosional velocities caused by the addition of *Heteromastus*. First, vertical tubes may reduce bioturbation caused by burrowing forms [127]. Second, microbial activity and binding may be stimulated. Third, fecal production may increase particle size, or mucus production may increase sediment

cohesion. Finally, tubes that extend above the surface layer may increase the thickness of the benthic boundary layer, thereby decreasing turbulence. Observations suggest that the last of these is an important mechanism, although the other three mechanisms have not yet been evaluated [110].

Rooted Aquatics and Macroalgae

Rooted aquatic vegetation often develops extremely large aboveground standing crops. Some representative values (dry wt/m^2) are: *Zostera*, 1–545 g [128]; *Thalassia*, 10–1800 g [129]; mangroves, 800–27,900 g [130]; and *Spartina*, 250–2100 g [131]. Not surprisingly, this aboveground structure baffles currents and reduces wave energy, although there are species-specific differences. Beds of *Spartina* and *Thalassia* reduced wave energy by 92% and 67%, respectively, over a distance of 20 meters [132]. Scoffin [133] found that a mangrove forest reduced a 40-cm/sec current to an unmeasurable velocity within 1 meter. As a result of reduced current velocities, vegetated areas usually have a greater percentage of silt–clay and organic content than unvegetated areas [133-135], although there are exceptions [72]. The stabilizing effect of seagrasses is demonstrated by the increased erosion after their removal [133, 134,136,137]. Destruction of a *Zostera marina* bed by cownose rays resulted in a net loss of 15–30 cm of sediment [136]. Reduction of marsh grasses due to an oil spill increased erosion 24 times over a nonimpacted area [138].

The extensive root and rhizome system of vascular plants binds sediment and increases shear strength. Shear strength in marsh clays is 2-4 times greater than in unvegetated clays [139]. Root configuration influences the degree of binding and, in general, dense horizontal root networks bind sediment more tightly than deeper, vertical root systems [41,140]. Marsh plants may be used to stabilize intertidal dredge spoils. Experimental planting of *Spartina alterniflora* stabilized spoils within two years, although development of a "typical" marsh ecosystem will take longer [141,142]. Seagrasses can be used to stabilize subtidal spoils [143], although some, such as *Thalassia*, are poor colonizers [129] and the logistics of transplanting or seeding are considerable.

In certain shallow-water areas, benthic algae form mats covering bottom sediments [127,133,144-146]. Mat-bound sediment in the Bahamas withstood currents 3-9 times greater than maximum tidal currents and 2-5 times greater than unbound sediment [146]. Different types of mats eroded at different velocities, although burrow holes or other discontinuities reduced the strength of all types of mats. However, Scoffin [133] found that algal mats did not greatly increase the percentage of silt–clay, nor were they as effective as seagrasses or mangroves in baffling currents. Additionally, algal mats may be ephemeral [133] or seasonal [127] features.

Effects of Particle Transport

Particle Redistribution

Sediment reworking causes horizontal and vertical redistribution of particles. There are three major kinds of redistribution: (1) reworking by vertically oriented species (conveyor belt species and funnel-feeders); (2) uniform mixing of the surface layer; and (3) particle movement along tubes or burrows. In each process, surface particles are initially transported to deeper sediment layers at rates exceeding sedimentation. The pattern of redistribution by vertically oriented species was described under the section entitled Particle Transport. Particle movement during construction of tubes and burrows is too variable to allow any generalized model. The eddy diffusion analogue can be used to model uniform mixing of the surface layer as described below.

When reworking is limited to a discrete mixed layer, the two-layer model of Guinasso and Schink [98] generates the vertical distribution for a single pulse of a particulate pollutant to the sediment surface. This model assumes an upper mixed layer and a deeper, historical layer with no reworking. The depth profile of a pulsed input depends on the ratio

$$G = D/Lv$$

where G = dimensionless mixing coefficient
D = biogenic diffusion coefficient, cm^2/sec
L = depth of the mixed zone, cm
v = sedimentation rate cm/sec

When G is small, a pulsed input of pollutants remain as a discrete layer that is buried by sedimentation of unpolluted sediment. Concentration of the pollutant remains high within this layer. After a longer period of time ($t > L/v$), most or all of the pollutant is buried below the mixing zone. Such conditions occur where there is little mixing, as in anoxic basins or areas where the sedimentation rate greatly exceeds the mixing rate. It is in these areas that the stratigraphic record is preserved and can be used to determine the temporal sequence of pollution events [147,148].

When G is large, i.e., rapid reworking compared to sedimentation, a pulse of pollutant is rapidly mixed throughout the biologically active layer. Concentration in the reworked layer is less than in the discrete polluted layer when reworking is slow, but more sediment is contaminated. As unpolluted sediment is deposited, the lower portion of the mixed layer is subducted below the depth of reworking, thereby reducing the total amount of the pollutant in the biologically mixed layer. Initially, the total amount of pollutant in the mixed layer will be lower when biogenic mixing is high. However, the decrease over time in

the pollutant approximates an exponential decay, so that measurable quantities remain in the biologically active zone for an extended period. The apparent "old age" of sediments in surface layers when dated by radioactive tracers [149] is consistent with this model.

Vertical redistribution of a pollutant modifies its chemical and microbial environment, especially if reworking extends below the RPD layer. Rates of microbial activity and degradation are generally lower under reducing conditions [150,151]. Formation of insoluble precipitates in the anoxic zone will reduce the bioavailability of certain pollutants [152,153] and may hasten their burial below the mixing depth. Conversely, transport of deeper particles to the oxidized layer will increase mobilization of other pollutants. Upward transport of sediments also reexposes pollutants covered artificially with uncontaminated sediment. In the absence of macrofauna, methyl mercury was released into the overlying water from the upper 1–2 cm of sediment in a freshwater system [154]. With the addition of tubificid worms or a clam, *Anadonta* sp, mercury was released from depths of 2.5 cm and 9.0 cm, respectively. Experiments similar to this study with marine sediment and species are needed to determine the feasibility of capping polluted dredge spoils with clean sediments.

Pelletization and Coprophagy

Fecal pellets of many filter- and deposit-feeders have high concentrations of nutrients and metals. Kraeuter [30] found that feces of common marsh deposit-feeders generally had higher concentrations of Mg, Mn, Zn and Mo than *Spartina alterniflora* or *Juncus roemerianus*, the major detrital sources. Concentrations of these elements as well as P were also higher in feces than in the sediment. Deposit-feeders often select finer particles [56,155] or organically encrusted particles [86], both of which may have high concentrations of sorbed pollutants. Concentrations of Co, As, Zn, Ca, Pb and Fe were 2.3–14 times greater in the feces of the kelp crab *Pugettia producta* than in kelp [156]. Because macroalgae often have high concentration factors, fecal deposition may represent a significant input of heavy metals into the sediment in areas where herbivory is common. In areas where fecal pellets are abundant, it would be informative to determine separately pollutant concentrations in unbound sediment and pellets.

Ingestion of fecal material or coprophagy is common in many invertebrate deposit-feeders, as well as in some fish [38,157]. For some species, fecal pellets may supply a substantial fraction of the metabolic requirements [38]. A species ingesting its own feces could increase its body burden and the retention time of a pulsed pollutant. Such an effect was demonstrated with a terrestrial beetle, in which individuals allowed to feed on their own feces retained more ^{65}Zn than individuals deprived of feces [158]. Ingestion of feces of other species may

be an important transfer mechanism between trophic levels and between pelagic and benthic systems.

In certain areas, deposition of feces from filter- and deposit-feeders is so great that surface sediments are largely composed of pellets. Such sediments are referred to as pelletized [5]. Table VI lists the contribution of feces to the surface sediments in some pelletized sediments and the dominant fecal producing organism(s). Fecal pellets usually form a layer <1–2.5 cm thick underlaid by a thicker layer of disaggregated pellets [47,161]. Packaging of finer material into sand-sized fecal pellets increases the effective sediment size and reduces the amount of unbound silt–clays. This increase in grain size increases porosity and the percentage of water, which can increase the erodability of the sediment, as discussed later. In muddy substrates, the reduction in sediment strength and increase in resuspension resulting from pelletization by deposit-feeders excludes filter-feeders. This is the trophic group amensalism hypothesis of Rhoads and Young [5,87]. Possible effects of this alteration in trophic structure include a reduction in biodeposition, an increase in resuspension and uptake of pollutants by a new suite of species.

The abundance of fecal pellets in a habitat represents the balance between rates of pellet production and disaggregation (or transport). Pseudofeces are loosely aggregated and break down rapidly [21,55], contributing little to pelletization. Certain pellets remain intact for months in the absence of mechanical disturbances such as waves or currents [55,162]; other pellets are largely degraded by microbes after 24 hours [163]. Pellets composed of carbonates are often more resistent because of cementation [159,164]. Both meiofauna [124, 165] and macrofauna [38] may disaggregate fecal pellets.

The relative contribution of feces from benthic filter-feeders, pelagic filter-feeders and deposit-feeders, and the rate of pellet disaggregation is hypothesized in Table III, as well as the overall potential for pelletization. It must be emphasized that there may be large differences in the degree of pelletization between habitats of the same general type. The potential is greater in muds and marshes because of low wave and current energy in both habitats and high densities of deposit-feeders in muds and epifaunal filter-feeders in marshes. The potential is lower in sandy areas because of the rapid breakdown of pellets and low in the deep sea because of the low rate of sediment reworking and low deposition rate of pelagic fecal pellets. Johnson's [114] observation that the highest proportion of recognizable fecal pellets occurs in deeper subtidal silts and the lowest in intertidal sands is consistent with our hypothesized sequence.

Digestive Alteration

In areas of high reworking, surface sediments are ingested several times a year [11]. Passage through the gut exposes particulate and sorbed pollutants

Table VI. Selected Pelletized Habitats

Location	Amount of Sediment as Pellets (%)	Dominant Producer of Feces	Comments	Reference
Bimini Lagoon	90% no.[a]	*Batillaria minima*	Calcareous	159
Buzzards Bay, Massachusetts	20% no.	*Nucula, Yoldia Nepthys*	Subtidal silt–clays	47
Dauphine Island, Alabama	40% (no.?)	*Crassostrea*	Quiet coves and *Spartina* marsh	28
Delmarva Peninsula, Virginia	40% wt[b]	–	Tidal flat, pellets from 18 species	28
Quisset Harbor, Massachusetts	40–50% no.	*Cumingia, Tellina, Nucula*	*Zostera* bed, 75% water at surface	72
Woods Hole, Massachusetts 26 stations	1–15% no.	–	Fine silt-medium sand, intertidal and subtidal	114
York River, Virginia	25% wt	*Crassostrea*?		160
Laboratory	70% wt	*Hydrobia ventrosa*	Silt-clays, 80,000/m^2	59
	15% wt	*Hydrobia ventrosa*	Silt-clays, 8,000/m^2	59

[a] no. = percent of particle number as fecal pellets.
[b] wt = percent of weight as fecal pellets.

to a harsh chemical environment. Digestive enzymes attack and degrade microbes and detritus and may release organically sorbed pollutants. The pH of the gut is often more extreme than in the environment and may fluctuate along the digestive system. In decapods, the stomach and midgut are acidic, while the hindgut is alkaline [28]. It has been demonstrated that the structure of some clay minerals is modified by digestive processes [28,166]. Presumably, digestion desorbs or chemically alters many pollutants, although the relative importance of this process compared to microbial and abiotic degradation is not known.

Sediment Strength and Water Content

Biogenic reworking alters the fabric (spatial arrangement of the particles) of a sediment; this , in turn, modifies other physical properties. Feeding and burrowing activities break up sediment aggregates and counteract compaction, thereby increasing the mean distance between grains and decreasing the number of grain-to-grain contacts. This creates an open sediment fabric. As a result, porosity and water content increase and compaction and bulk density decrease. These changes in porosity and packing also modify tortuosity, which alters the rate of molecular diffusion. Aggregation of silt-clays into sand-sized fecal pellets also creates an open-fabric, high-water-content sediment. In general, an increase in the water content reduces sediment strength. At water contents $\leq$50%, muds display plastic-dilatant properties [167]. When water content exceeds 50%, high clay content (>50%) muds display thixotropic or fluid properties. Thixotropic sediments display fluid properties (i.e., flow) in response to physical stress and have very low bearing capacities.

There is good observational and experimental evidence that reworking increases the water content of subtidal muds. Water content of the surface 5 mm in areas with dense populations of protobranchs is characteristically $\geq$60% and often >70%, whereas less intensively reworked areas have water contents of 30-50% [168,169]. Addition of *Nucula proxima* and *Yoldia limatula* to aquaria increased water content of the upper 5–10 mm of sediment by about 8% [101,169]. The deeper feeding *Molpadia oolitica* maintained a water content of 60% to depths of 26-30 mm [87].

Reworking does not always increase porosity. Cadee [85] reported that *Arenicola marina* did not influence the water content of intertidal sand, even though density of this active reworker was high. In a laboratory aquarium, *Leptosynapta tenuis* had no measurable effect on sediment compactness (=shear strength) in the top 0- to 2-cm interval, but decreased compactness slightly in the 2- to 10-cm interval [11]. Using his own and Myer's [11] data, Powell [20] suggested that reworking by *Leptosynapta* actually increased compaction and stabilized the sediment. These three studies were in sandy substrates, which compact more rapidly than silt-clays [170]. It seems likely, then, that the

effect of reworking on water content is a function of grain size. If the rate of compaction is less than the rate of biogenic displacement, reworking will modify porosity. However, if the rate of compaction is greater than the displacement rate, reworking will not strongly affect compaction or porosity. This conceptual framework may be useful in predicting the effect of reworking on porosity in different sediments and at different depths within the sediment. It is also possible that the water content of intertidal sediments is lower than similar subtidal sediment because of increased drainage and compaction during low tide.

Erosion and Resuspension

The transport and ultimate horizontal distribution of particulate and sorbed pollutants depends on sediment stability. At least three effects of biogenic processes can significantly decrease bottom stability and increase the potential for erosion. These are: (1) an increase in water content; (2) a disaggregation of organic matrix; and (3) a modification of surface topography.

One of the most important mechanisms increasing the erodability of fine sediments ($<100\ \mu$) is an increase in porosity. Laboratory studies have demonstrated that the current velocity needed to initiate erosion (critical erosion velocity) decreases with increasing water content, although there are considerable differences between experiments [171]. The reduction in sediment stability is at least partially a function of the reduction in the number of grain-to-grain contacts and electrostatic attraction [170]. Pelletized surfaces are easily eroded because of their high water content and low bulk density. Additionally, the granular nature of a pelletized surface may increase turbulence [169]. Pelletized sediments should have lower critical erosion velocities than sediments with a size distribution similar to the fecal pellets of the pelletized sediment.

Physical disruption of sediment during reworking may break up the organic matrix binding particles [110,111]. Yingst and Rhoads [111] suggested that the rate at which macrofauna and meiofauna broke up the organic-mineral aggregates partially determined seasonal changes in erodability. Such a mechanism could be important in either muddy or sandy substrates. One difficulty with this hypothesis is that organic mucus is very elastic and coalesces after passage of small organisms [113]. Besides physical disruption, deposit-feeders may reduce the density of bacteria and microflora, thereby reducing the rate of microbial binding. Certain organisms eject particles directly into the water column, either during feeding (e.g., *Yoldia*, [58])or burrowing (e.g., *Callianassa* [84]), which could result in resuspension and transport of silt-clays.

Microtopography increases turbulence at the sediment-water interface and, hence, erosion. It has been observed in laboratory [169] and *in situ* [116] studies that erosion begins at small biogenic structures. Turbulent flow caused by burrow apertures results in small-scale plucking of sediment in marshes [41]

and intertidal fecal mounds are eroded each tidal cycle [11]. Mounds, tracks and fecal ropes, which are common in the deep sea [71] may serve as "catalysts" for erosion by periodic bottom currents [67,172]. Microtopography appears to be an important process in initiating bed load transport and, in some cases, resuspension in both deep- and shallow-water sites.

Laboratory evidence that infaunal organisms increase erosion includes the observations that both *Yoldia limatula* and *Nucula proxima* increased resuspension in aquaria [101,169]. After 60 days of reworking by a natural assemblage of benthic organisms, critical erosion velocity decreased by ≈60% from the initial value [116].

Field evidence also demonstrates that various biogenic activities initiate resuspension in muddy substrates. Reworking by a *Nucula-Nephtys* deposit-feeding assemblage reduces sediment stability enough that relatively weak tidal currents resuspend surface sediments, resulting in a bottom turbidity zone that covers much of Buzzards Bay [87,173]. Resuspension appears limited to the upper 1 cm of sediments [169,174]. Resuspended material consists of both fecal pellets [175] and benthic microalgae as indicated by the increase in chlorophyll-a [175-177]. A spill of diesel fuel oil reduced the density of deposit-feeders in Buzzards Bay [5]. As a direct result of the reduction in deposit-feeding bivalves or as an indirect result of stabilization by colonizing tubicolous polychaetes, the sediment became firmer and no bottom turbidity layer was observed.

Rates of resuspension over intensively reworked sediments can be extremely high. Table VII lists resuspension rates and dominant sediment reworkers for selected habitats. These rates are based on near-bottom sediment traps, which more closely measure the rate of resuspension than input of new material [182]. Although design and height off the bottom of the settling traps differed between studies, several patterns are suggested by these data. Reworked silts and silty sands have greater resuspension rates than fine sands. This is contrary to the often reproduced Hjulstrom diagram [183], which indicates that fine sands have the lowest threshold velocities. Young and Southard [116] observed that bioturbated muds had lower threshold shear velocities than fine sands, which is consistent with the resuspension data. Furthermore, particles $\geq$0.1 mm are more apt to be eroded by bed load transport, whereas finer particles are suspended [184].

Composition of the fauna appears to have a major effect on the rate of resuspension. Resuspension rates in areas populated by *Molpadia oolitica* were about three to four times greater than those in the highly reworked but topographically smooth Buzzards Bay sediments (Table VII). Fecal mounds of *Molpadia* increase bottom roughness, which probably increases turbulence and bottom scour [87]. The potential effect of excavator species is suggested by the increased resuspension in areas populated by *Callianassa* [61]. We suspect that

Table VII. Resuspension Rates

Location	Deposition Rate ($mg/cm^2/day$)	Depth (meters)	Height of Trap above Bottom (cm)	Dominant Reworkers	Comments	Reference
Buzzards Bay, Massachusetts						
Station R	95 ml ($\approx$14 $mg/cm^2/day$)	20	10	*Yoldia, Nucula* tellinids	Silt-clay	169
Station P	55 ml ($\approx$ 8 $mg/cm^2/day$)	10	10	*Ampelisca*, tubed polychaetes	Silty-sand	178
Cape Cod Bay, Massachusetts						179
Station 1518	66-87	34	20	*Molpadia*	Sandy silt	
Station 2318	1.5-2	12	20	*Polydora, Unciola, Protodrilus*	Silt	
Discovery Bay, Jamaica						61
Station A5	19	2	7	*Callianassa* $30/m^2$	Loose sand, mounds common	
Station A5	1.1	2	50			
Station B5	6	2.1	7	*Callianassa* $10/m^2$	Sand bound by algae, mounds common	
Station B5	0.73	2.1	50			
Station C1	0.45	4	50	?	Veneer of sand, no mounds	
Las Maritas, Venezuela	0.45-1.1	4?	20	*Onuphus, Megalomma*, spionids	Fine-medium sand	180
Long Island Sound						181
Summer	250.5	14	15	*Nucula, Yoldia Tellina*	Silty sand	
Winter	121.4	14	15			

Table VII, continued

Location	Deposition Rate ($mg/cm^2/day$)	Depth (meters)	Height of Trap above Bottom (cm)	Dominant Reworkers	Comments	Reference
Narragansett Bay, Rhode Island						
Lower Bay	5.1	7	100	*Nucula, Mercenaria*	Sandy silts to gravel–silt–clay	182
Mid-Bay	3.1	7	100	*Glycera, Tellina*	Silty sands to sand–silt clay	
Upper Bay	2.0	7	100	*Mulinia*	Sand to silty sand	

the species resulting in the greatest resuspension are those that create mounds (funnel-feeders, some conveyor-belt species and excavators) and species that continually mix the upper layer, such as protobranchs and, to a lesser degree, some vagile surface deposit-feeders.

Resuspension increases the rate of flux of pollutants between the sediment and water as well as horizontal dispersion of a pollutant. Aller and Cochran [75] have proposed a sequence of resuspension and sorbtion to explain the excess ^{234}Th in Long Island Sound sediments. Resuspended low-activity particles, i.e., low concentration particles, or microalgae scavenge pollutants from the water column. Settlement and subsequent biogenic reworking of these particles mixes the now high-activity material within the surface layer. Reworking also exposes deeper low-activity material to resuspension. This process may describe the cycling of many pollutants, which are bound by organic matter or microalgae. Resuspended material may also transfer pollutants to the water. Reduction in the ambient concentration of a substance may increase the rate of diffusion from resuspended particles. Resuspension of reduced particles will result in the oxidation and mobilization of certain compounds [75]. Finally, resuspension makes polluted sediment available to pelagic and benthic filter-feeders.

Although various lines of evidence indicate that reworking influences erodability, its exact role in controlling temporal-spatial variations in resuspension is less clear. Station Q in Buzzards Bay was highly reworked, yet there was little resuspension at this station [169]. Presumably this reflects lower current velocities at this site. In two years, minimum critical rolling velocities occurred during the summer, a period of high biogenic reworking; the maximum critical velocities occurred during the late-fall/winter, a period of lower reworking [110]. However, in 1976 the exact opposite trend was observed with maximum and minimum critical velocities occurring in July and October, respectively. The increased stability during the summer of 1976 may be the result of a dense settlement of the tubicolous polychaete *Owenia fusiformis*. Cause(s) for the lower stability in the winter of 1976 is not known. Using a sophisticated *in situ* flume in Buzzards Bay, Young and Southard [116] found that small-scale heterogeneity in critical erosion velocities exceeded any possible seasonal cycles, even though reworking rates are highly temperature dependent. Finally, there was no significant correlation between critical erosion velocities and a biogenic sediment processing coefficient [111]. The inability to predict qualitative results from some of the most intensively studied sites in the world suggests that we are a long way from understanding the biogenic mechanisms influencing the transport of particulate pollutants.

Fluid Transport

Although little is known about the mechanisms, rates or effects of biogenic fluid transport, recent studies suggest that it is more important than particle

transport in controlling the distribution and flux of many dissolved compounds. Molecules transported include O_2, H_2S, nutrients, trace metals and soluble pollutants. Biogenic activities resulting in fluid transport include burrowing by vagile fauna and irrigation by vagile and stationary fauna. Irrigation is the transport of water through a tube or organism for respiratory or feeding purposes.

When a highly mobile fauna is restricted to the surface layer, its activities tend to homogenize or mix pore waters within the biologically active layer. In such cases, the rate of fluid transport can be described by an effective diffusion coefficient [9,101,102]. The influence of biogenic fluid transport on pore water distribution depends on the ratio of the effective biogenic diffusion coefficient (D_1) to the molecular diffusion coefficient (D_2). If $D_1 \approx D_2$, biogenic activities have little effect. However, if $D_1 > D_2$, biogenic fluid transport activities significantly modify pore water distributions and flux rates. Sensitivity of pollutants to biogenic fluid transport activities is directly related to their molecular diffusion rate.

The potential importance of biogenic fluid transport by mobile fauna is indicated by recent work on *Yoldia limatula* [101]. *Yoldia* modified the pore water distributions of Fe, Mn, Ca, $HPO_4^=$, alkalinity and NH_4^+, although not all in the same manner. It also increased the rate of flux of NH_4^+, Fe and Mn from the sediment to the water. As a result of the loss of soluble phases to water, concentrations of these ions within the mixed layer were reduced. Increased flux of Fe and Mn is especially significant because they precipitate as oxides, which scavenge certain compounds from the overlying water. The effective diffusion coefficient based on pore water profiles for *Yoldia* was $\approx 1 \times 10^{-5}$ cm^2/sec, about five times greater than the biogenic diffusion coefficient based on particle transport. The difference between these two rates is apparently due to the effects of fluid transport during irrigation and burrowing. Aller [9] suggested that, in general, the effective biogenic diffusion coefficient for fluid transport is about 10 times greater than the biogenic diffusion coefficient for particles. Whether this conclusion holds for soluble pollutants remains to be tested.

In stationary fauna and vagile fauna less active than *Yoldia*, irrigation is a major or sole form of fluid transport (Table VIII). Extrapolations of the rates in Table VIII to the field should be treated with caution because of laboratory artifacts, methodological differences and the influence of environmental factors on irrigation rates. The influence of environmental factors and body size discussed under biodeposition rates will apply in general to irrigation rates.

The significance of the rates in Table VIII is illustrated by comparing the volume of water transported during particle reworking versus irrigation. Particle working transports the pore water entrapped within the sediment. Using the data of Rhoads [47] and Mangum [49] for *Clymenella torquata*, it is

Table VIII. Irrigation Rates of Infaunal Species

Species	Guild	Individual Rate (ml/ind/hr)	Comments	Reference
Annelids				
Amphitrite ornata	SISDF	74.6	3,500 mg/ind.	185
Arenicola marina	FUN	50	Maximum rate, small ind.	186
Arenicola marina	FUN	42–250	8.8 g/ind.	48
Clymenella torquata	CB	2–4		49
Malacoceros fuliginosa	SISDF	2	Maximum rate	186
Myxicola infundibulum	SIFF	270	2,700 mg/ind.	187, 188
Nereis diversicolor	MISDF-V	37	Maximum rate	186
Sabella pavonina	SIFF	74	190 mg/ind.	187, 188
Schizobranchia insignis	SIFF	70	1,000 mg/ind., feeds most of the time	187, 188
Bivalves				
Arctica islandia	MIFF	339–6,561	11-1,310 mg dry wt ind.	35
Cardium edule	MIFF	949–3,397	28-173 mg dry wt ind.	35
Mercenaria mercenaria	MIFF	180-5,570	43 mm/ind., 12° C – 88 mm/ind., 25° C	32
Mya arenaria	MIFF	347–1,800	100–5,000 mg/ind.	34
Venerupis pullastra	MIFF	1,290	2.68 g wet wt/ind.	37
Crustaceans				
Corophium volutator	MISDF-V	76	Maximum rate	186
Echinoderms				
Echinocardium cordatum	MISSDF-V?	90	5–5.7 cm/ind. in sand, maximum rate	186
		13	2.5–3 cm/ind. in mud, maximum rate	
Echiurids				
Urechis caupo	MIFF?	1,800	60 g/ind.	189

possible to calculate the volume of water transport per individual per day by particle transport as 0.41 ml. The amount of water transported per day by irrigation is 48-96 ml, or 117-234 times greater. Similar calculations using data of Renfro [190] and Foster-Smith [186] indicate that *Nereis diversicolor* transports 677 times as much water by irrigation as by burrowing. These calculations are fairly crude and may overestimate the actual difference; however, it is clear that much greater volumes of water and their dissolved ions are transported by irrigation.

The effect of irrigation depends not only on flowrates, but also on the permeability of the tube or organism. Because of incomplete mantle fusion, protobranchs "leak" water into the sediment [101]. Mantle fusion is more complete in eulamillibranch bivalves, which allow little water exchange with the sediments, even though flowrates are high. Parchment tubes such as those made by *Chaetopterus* appear impervious to water, whereas mud or sand tubes allow some exchange of tube and pore water. Foster-Smith [186], presents an interesting discussion of the hydrodynamics of water flow through animals and their tubes and the differences in permeability among species.

The influence of the tubicolous polychaete *Clymenella torquata* on pore water chemistry was studied in laboratory experiments [101]. *Clymenella* did not feed during these experiments, thus the observed changes were a result of irrigation and tube construction. Sediments with *Clymenella* had higher pore water concentrations of Fe and Mn in the top ≈2 cm, but lower concentrations from 2-12 cm and an increased rate of flux of Mn, Fe, NH_4^+ and $HPO_4^=$. Exchange of tube and pore waters and diffusion of ions through the tubes probably were the major processes resulting in these modifications. Grundmanis and Murray [191] suggested that the anomalous pore water concentrations at a depth of 20-30 cm in Puget Sound were a result of irrigation by maldanid polychaetes.

The wall of well-irrigated, permeable tubes or burrow walls represent vertical extentions of the sediment-water interface into the sediment body. Closely spaced tubes or burrows increase the total area of the sediment-water interface and decrease the average distance an ion must travel to be transported to the water column. In areas of dense tubicolous populations, surface area in the tubes may exceed the planar area of the sediment surface. Because lateral diffusion into tubes results in a fixed three-dimensional diffusion geometry versus the one-dimensional geometry resulting from burrowing and molecular diffusion, vertical or one-dimensional diffusion coefficients are inappropriate. Instead, horizontal diffusion coefficients should be calculated from a radial-diffusion model [101] (see Table V for comparison with *Clymenella*).

Few studies have examined the influence of organisms on the loss rate of pollutants from marine sediments. Addition of *Nereis diversicolor* to contaminated sediments increased the loss rate of ^{65}Zn three to seven times compared to sediments without worms [190]. The increased loss could be due to: (1) in-

creased surface area from burrowing; (2) irrigation of burrows; or (3) particle transport. Artificial agitation of the sediment increased the loss of ^{65}Zn 3.25 times. The lower loss rate by artificial particle transport suggests that increased surface area or irrigation by *Nereis* contributed significantly to the diffusion loss of ^{65}Zn. Bryan [192] suggested that burrowing organisms would release heavy metals dissolved in interstitial water. Irrigation by *Arenicola marina* [193] and *Uca pugnax* [92] may have contributed to the degradation and dissipation of buried oil. Further studies similar to those mentioned here are needed to quantify the influence of benthic organisms on the flux of pollutants from the sediment. More sophisticated experiments will be necessary to determine the relative importance of different processes promoting the loss of pollutants from sediments.

Biogenic fluid transport also increases oxygen concentration and Eh of surface sediments. Molecular diffusion oxygenates only the top 1-2 mm of mud bottoms, yet the oxidized layer in bioturbated muds can extend ≥30 mm [5, 161]. Observational and experimental data have demonstrated that a wide variety of feeding-mobility guilds inject oxygen into deeper sediments: funnel-feeders [46], conveyor-belt species [87], excavators [194], vagile burrowers [11,102] and tubicolous fauna [16,90]. Surface fauna such as protobranchs depress the RPD layer uniformly. Tubicolous fauna and deep burrowing vagile polychaetes, e.g. *Nephtys* and *Scoloplos*, create oxidized microhabitats ("halos" [11]) within the reduced layer. By depressing the RPD layer either uniformly or in distinct shafts, fluid transport increases the amount of pollutant exposed to an aerobic environment.

Selective Uptake of Ions by Rooted Aquatics

Absorption of compounds through the leaves of rooted aquatic vegetation [195,196] and then transport into the sediment through the detrital pathway may represent a transport mechanism for certain nutrients and pollutants. A potentially more important mechanism is the uptake of nutrients or pollutants through the roots, which then may be excreted into the water, recycled back into the sediment by means of detritus, or enter the detrital food web. Among the elements pumped from the sediment are P, N, Zn, Fe and Ca [196-199]. Transport by aquatic plants can result in considerable fluxes. Net flux of P from the sediment to *Zostera marina* was 107.5 mg/m^2/day, and the net flux from the leaves to the water was 62.4 mg/m^2/day [198]. Rooted aquatics may concentrate pollutants from the sediments, as demonstrated by the high concentrations of mercury in *Spartina alterniflora* [200]. Whether transport through rooted aquatics results in a net gain or loss from the sediment will depend on the nutrient or pollutant, the species of plant and environmental conditions. Available evidence suggests that rooted aquatics more often "pump" pollutants from sediment.

Macrofaunal-Microbial Interactions

Microbial degradation is a major pathway by which many pollutants are removed from the environment. Three macrofaunal activities that increase microbial density and metabolism are irrigation, fecal pellet production and tube construction. By increasing oxygen input into the sediment and, perhaps, organic or nutrient content, irrigation stimulates aerobic microbes. Irrigation by *Abarenicola pacifica* stimulates microbial activity at the head end of the worm, a process Hylleberg [46] termed "gardening." Rhoads et al. [174] extended this concept to suggest that fluid transport activities by subsurface deposit-feeders, e.g., *Nucula* and *Nepthys*, increased microbial activity within the entire reworked layer. *Yoldia limatula* appeared to stimulate microbial activity below the feeding zone, perhaps by flushing out inhibiting metabolites [101]. Stimulation of microbial degradation by *Arenicola marina* may contribute to the loss of oil from sediments [193].

Feces of several invertebrates increase in organic and/or nitrogen content due to microbial colonization after egestion [157,201,202]. Feces of 10 species of invertebrates had higher rates of oxygen consumption than either the undigested food or sediment, again suggesting increased microbial activity [203]. Causes for enhanced microbial activity are not well understood but might include: (1) cropping of senescent individuals; (2) increased organic or nutrient content due to mucus, excretions or destruction of microflora; (3) selection by deposit- or filter-feeders of finer organically coated particles; or (4) diffusion of microbial waste products. High concentrations of at least some pollutants in feces and the enhanced microbial metabolism tentatively suggest that fecal pellets are foci of microbial degradation of pollutants.

Recent work on *Amphitrite ornata* suggests that tube and burrow walls also are sites of enhanced geochemical and microbial activity [16]. This large terebellid polychaete constructs a muddy tube composed of an oxidized inner wall about 3 mm thick and an anaerobic outer wall about 10 mm thick. Organic matter, acid-volatile sulfides, nonvolatile sulfur, Fe, Mn and Zn are all enriched in the tube wall compared to ambient sediment. The high concentrations of oxides of Fe, Mn and Zn may scavenge metals as water is pumped through the tube. Tubes release NH_4^+, Fe, $HPO_4^=$ and possibly Mn and ATP into the water. The flux of NH_4^+, $HPO_4^=$ and Fe is 1–10% of the total flux in Long Island Sound, even though *Amphitrite* tubes constitute only a small proportion of the surface area. These fluxes apparently are due to diffusion through the tubes and microbial decomposition within the tube wall. Below 1 cm, meiofaunal density, ATP and dehydrogenase activity (DHA) appear higher in tube walls than surrounding sediment, which is consistent with enhanced microbial activity. In the outer wall, sulfate reduction is the major decomposition process, with rates exceeding the surrounding sediment. The authors concluded that the tube "retains along

its entire length diagenic properties typical of, or more intense than, the sediment-water interface." Most tubicolous species have tubes much thinner than *Amphitrite*, and it is unclear whether these results are applicable to such tubes.

Pollutant Effects on Rate of Bioturbation

Pollutant stress can modify the types of bioturbation and reduce rates of reworking or irrigation. Filtration rate of *Mytilus edulis* decreased in response to dissolved Cu, Zn, Hg, cyanide, thiocyanate and sulfide [204]. Concentrations required to reduce filtration rate by 50% ranged from 0.04 mg/l for Hg to 84 mg/l for thiocyanate. Reduced filtration rates in response to pollutants have been reported for *Geukensia (Modiolus) demissus* [205], *Crassostrea virginica* [206] and *Mya arenaria* [34]. Partially as a result of reduced filtration rates, *Mya* in an oiled site gained only 50% as much carbon as a control population [207].

The time required for *Macoma balthica* to reburrow was greater in sediments containing high levels of heavy metals [208]. Reburrowing time of various bivalves increased in response to the water-soluble fraction of crude oil [209], dissolved copper [210,211] and phenol [211]. Presumably, reduced reburrowing ability indicates a reduction of the rate of burrowing within the sediment. *Uca pugnax* constructs abnormally shaped and shallow burrows in oiled sediment [212]. Avoidance of polluted sediment by aquatic invertebrates [208,209, 212] may result in lower bioturbation rates in patches of polluted sediment. The sediment reworking rate of *Arenicola marina* was reduced 46–93% in sediment-bound oil [193] with the percentage reduction related to the aromatic content of the oil. Sediment turnover by *Arenicola cristata* after 144 hours was more than 8 times greater in controls than in tanks with 150 μg/l of methyl parathin [214]. In sediments of low permeability, a reduction in reworking could restrict a pollutant to the upper most sediment layer. In porous sediment, reduction in reworking could decrease the turnover of pollutants in deep layers and the oxidation of buried pollutants.

Pollutant stress also can modify the rate of bioturbation by altering community composition. Pearson and Rosenberg [215] suggested that as organic enrichment increases, abundance of excavators and large mobile species declines, while less active species (sedentary surface deposit-feeders, conveyor-belt species and small filter-feeding bivalves) increase. The originally complex three-dimensional sediment structure "tends, therefore, toward laminar stratification," with the aerobic layer confined to a narrow zone. At higher organic inputs, the community is dominated by small opportunistic polychaetes, e.g., *Capitella*, which have low reworking rates. Additionally, the relative abundance of "non-selective" subsurface deposit-feeders increases. Initial recolonization of dredge spoils [124] and experimental plots [181] in Long Island Sound was by shallow-

burrowing, filter-feeding bivalves and tubicolous surface deposit-feeders. Activities of these initial colonizers produced a porous surface layer of fecal pellets and depressed the RPD layer to ≈1 cm [124]. Subsequent colonization by deep-burrowing fauna and subsurface deposit-feeders increased water content and decreased the RPD layer to 2-3 cm.

SUMMARY

The major biogenic processes modifying sediments are biodeposition, particle transport, fluid transport, stabilizing mechanisms and macrofaunal-microbial interactions. We have at least a basic understanding of the mechanisms and rates of biodeposition and particle transport, but this knowledge is lacking for the last three processes, even though in many habitats they may be more important than biodeposition or particle transport. In particular, fluid transport, biogeochemical processes in tubes, fecal pellet-microbial interactions, and microbial binding may prove to be key processes in many habitats. Table IX summarizes the primary effects of biogenic acitivities on sediment parameters. Although based on limited data, the table can be used as a guide to bioturbation processes and to predict general trends.

The basic research reviewed here strongly suggests that biodeposition and bioturbation can have a major impact on the rate of flux of pollutants between water and sediment and on the distribution of pollutants within sediments. Basic and applied research has provided some insights into the effects of bioturbation on the dynamics of nutrients and trace metals. By contrast, little is known about the effects of bioturbation on the flux of petroleum or pesticides from sediments. Research by Gordon, Dole and Keizer [193] provides an example of the type of investigation needed in this area.

Reworking of sediments in many habitats is dominated by a few species either because of their size or density. Thus, the research needed to understand the effects of bioturbation on pollutants within any community can be limited to key species. Our challenge now is to identify the key species and quantify the mechanisms of sediment modification.

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Table IX. Qualitative Effects of Biogenic Activities on Sediment Parameters

Biogenic Activity/ Sediment Parameter	Deposition of Particles	Porosity	Particle Distribution	Erosion and Resuspension	Homogenize Surface Layer	Bury Surface Sediment	Expose Deep Sediment	Area of Sediment-Water Interface	Depth of Aerobic Layer	Flux of Ions from Sediment	Microbial Activity	Spatial Heterogeneity
Filter-feeders[a]	++[b]	0[c]	0	0	0	0	0	0	0	0	0	0
Surface Deposit-feeders[a]	0(+)[d,e]	+(++)	Disaggregation of pellets and flocs	+	+(++)	0	0	0	+	+	- to +	- (high density)
Subsurface Deposit-feeders[a]	0	+(++)	Disaggregation of pellets and flocs	0 to ++	+(++)	+	+	0	+	+	- to +	- (high density)
Conveyor-Belt Species[a]	0	+	Biogenic graded bedding, winnowing of fines	+	+	++	++	0	+	+	- to +	- (high density) + (low density)
Funnel-feeders[a]	0	- to + (depth dependent)[f]	Biogenic graded bedding, winnowing of fines	+(-?)	+	+	+	0	+	+	- to +	- (high density) + (low density)
Burrowing	0	+(++)	Disaggregation of pellets and flocs	+(++)	++	+	0(+)	+	+(++)	+(++)	+	-
Excavation[g]	0	+	Biogenic graded bedding, winnowing of fines	+(++)	+	+(++)	++	++	+(++)	+(++)	+	- (high density) + (low density)
Tubes[g]	+(++)	0(+)	Vertical aggregation	-	?	0(+)	0	++	+	++	++	+
Fecal Pellets	0	+(++)	Increase mean size	++	+	0	0	0	+	0(+)	++	- (high density)
Digestion	0	0	Disaggregation	0	0	0	0	0	0	0	- to +	0
Irrigation	0	+	0	0	0	0	0	0	++	++	++	+ (low density)
Microtopography	0(- ?)	0	Winnowing of fines	++	0		0	+	0	0	0	+
Disturbance by Epibenthos	0	0	0	+	+	0(+)	+	+	0	0	0	+
Macrophytes	++	+?	Increase in fines	-	?	0	0	0	+?	++	+?	- (high density) + (low density)
Microbes	0	0	Agglutination of fines	-	0	0	0	0	-	+?	++	0(+)

[a] Only direct effects of feeding activity are included; effects of fecal pellet production, burrowing, etc., are considered separately.
[b] ++ = activity greatly increases sediment parameter.
[c] 0 = activity has no or minor effect on sediment parameter.
[d] + = activity increases sediment parameter.
[e] ( ) = indicates occasional importance.
[f] - = activity reduces sediment parameter.
[g] Includes construction, maintenance, diffusion and processes within walls.

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